Nomenclatural Changes and New Taxa in Claytonia (Portulacaceae) in Western North America

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Claytonia here includes all annual ABSTRACT. Montia species with principally basal leaves and scapiform inflorescences bearing one pair of free or fused cauline leaves. Three morphologically distinctive diploids define the basic species of a polymorphic polyploid complex formerly named C. perfoliata sensu lato. In this complex, we propose two new subspecies, C. perfoliata subsp. intermontana and C. parviflora subsp. grandiflora, and four subspecific combinations. A perfoliate-leaved subspecies of C. exigua is newly recognized.

(Howell) Tidestrom to the above list of recognized species that were earlier assigned to Montia. The latter genus, while still diverse (nine sections for only 13 species, as recognized by McNeill (1975)), differs from Claytonia in having numerous stem leaves, which may be alternate or opposite, in lacking a basal leaf rosette, and in having pantocolpate pollen rather than the trizonocolpate type characteristic of Claytonia. In habit, Montia species are annuals or rhizomatous to stoloniferous perennials, lacking the fleshy taproots or tuberlike underground storage organs seen in many perennial species of Claytonia. The group of taxa that had previously been united as the polymorphic species Claytonia perfoliata sensu lato was shown by Miller (1976, 1978) to be a polyploid, largely autogamous pillar complex based upon three morphologically distinct diploid entities (n = 6). When raised to species rank, these entities fall within the already named taxa C. perfoliata, C. parviflora, and C. rubra. Together with the putatively ancestral diploids, each of these species includes a variable array of eupolyploids ranging from tetraploid to, in some cases, as high as decaploid (Miller, 1978). Many polyploid races have intermediate morphologies suggestive of an alloploid origin, but some races, especially at the tetraploid level, are scarcely distinguishable from the basic

Through the work of Swanson (1966), Nilsson (1967), McNeill (1975), and others, the genus Claytonia is coming to be accepted in a more inclusive sense than was common in monographic and floristic works of the first half of this century (e.g., Howell, 1893; Pax & Hoffmann, 1934; Ferris, 1944; Hitchcock, 1964). In what now seems to be an unjustified generic split, certain taxa of rhizomatous perennials and annuals that were classified in Claytonia prior to 1893 had been segregated into Montia. Morphological evidence including pollen (Nilsson, 1967), growth habit (Swanson, 1966), and chromosome numbers (Lewis & Suda, 1968; Fellows, 1975; Miller & Chambers, 1977), along with numerical taxonomic analysis (McNeill, 1975), now places the following former Montia species more naturally in Claytonia: C. arenicola L. F. Henderson, C. cordifolia S. Watson, C. exigua Torrey & A. Gray (= C. spathulata Douglas ex Hooker, nom. illeg.), C. gypsophiloides Fischer & C. A. Meyer, C. perfoliata Donn ex Willdenow, C. saxosa T. S. Brandegee, and C. sibirica L. These taxa differ from Montia, as redefined by McNeill (1975), in having their principal leaves in a basal rosette and in possessing inflorescences borne on scapelike stems with only a single pair of cauline leaves, which may be united into a bilobed or toothed disk. We propose to add C. parviflora Douglas ex Hooker and C. rubra

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diploids and may be intraspecific autoploids.

Our taxonomic proposal for the C. perfoliata complex sensu lato is to recognize as species the three taxa mentioned above and to divide each species into a limited number of broadly defined subspecies. Within each species, one subspecies contains the basic diploid races along with polyploids that are scarcely distinguishable from them. The one or more remaining subspecies are framed around clusters of morphologically similar polyploid races, usually having a more or less well defined geographical range. The following lectotypifications, new taxa, and new combinations are necessary for this taxo-

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nomic revision. Claytonia exigua subsp. glauca, C. parviflora subsp. grandiflora, C. parviflora subsp. viridis, C. perfoliata subsp. mexicana, and C. rubra subsp. depressa appeared earlier in The Jepson Manual (Hickman, 1993) and are here being validated.

Claytonia perfoliata Donn ex Willdenow, Sp. Pl.
1: 1186. 1798. Limnia perfoliata (Donn ex Willdenow) Haworth, Syn. Pl. Succ. 12. 1812.
Montia perfoliata (Donn ex Willdenow) Howell, Erythea 1: 38. 1893. TYPE: Herbarium Willdenow No. 4984, Cl. perfoliata 2, Mus.
Bot. Berol. Film Nr. 816a (lectotype, here designated, B-W [photograph seen]).

& K. Hoffmann, Nat. Pflanzenfam. ed. 2 16c: 259. 1934. *Claytonia platyphylla* (Rydberg) Holub, Preslia 47: 328. 1975. TYPE: U.S.A. California: [Santa Barbara County,] Gaviota Pass, *Brewer 384* (holotype, US).

Limnia guadalupensis Rydberg, N. Amer. Fl. 21: 311. 1932, syn. nov. TYPE: Mexico. Baja California: Guadalupe Island, Palmer 15 (holotype, NY; isotypes, F, NY).

The diploid elements of the above subspecies were characterized by Miller (1978: figs. 6–9) as having linear juvenile leaves and broadly deltate, mucronate adult leaves; their fully perfoliate cauline leaf disk has two mucronate teeth. Together with related polyploids they range widely through the Coast Ranges of California to Baja California, Arizona, and mainland Mexico, reaching the highlands of Guatemala.

Authorship of this well-known name is often attributed to James Donn, who, however, only published it as a nomen nudum. Of the three sheets in Willdenow's herbarium, those numbered "1" and "2" each hold a beautifully prepared specimen, probably of garden origin. We select the sheet numbered "2" as the lectotype. A third sheet consists of four fragments only; one of these is a teratological inflorescence with separate cauline leaves, which evidently entered into Willdenow's description, in part. This "inaccuracy" (Sims, 1811) may have led to some confusion about Willdenow's plant among contemporary botanists, who were familiar with the typically perfoliate-leaved species because of its rapid, spontaneous spread among European botanical gardens after being introduced to Kew Gardens in 1796. The date and place of introduction were given by Sims (1811), who credits Archibald Menzies as the discoverer of the species. There is a sheet at BM on which three specimens are marked as having been collected by Menzies on the "North-west coast of America. 1792-3-4" (Photo No. 917-1, NY).

Claytonia perfoliata Donn ex Willdenow subsp. intermontana Miller & Chambers, subsp. nov. TYPE: U.S.A. Nevada: Churchill County, Highway 50, 8 mi. E of Eastgate, 7 mi. W of Carroll Summit, 2n = 24 [by J. R. Swanson], H. K. Sharsmith 4767 (holotype, OSC).

A subsp. *perfoliata* caulibus foliisque patulis vel erectis saepe rubello-viridis, discis perfoliatis saepe hemidivisis differt; a subsp. *mexicana* caulibus foliisque saepe rubelloviridis, foliis adultis ovato-rhombeis vel subdeltatis raro mucronatis, discis perfoliatis saepe hemidivisis differt.

Claytonia perfoliata Donn ex Willdenow subsp. mexicana (Rydberg) Miller & Chambers, comb. nov. Basionym: Limnia mexicana RydPlants annual, 2–20 cm tall, often red-pigmented (shade-grown plants usually green); stems and leaves erect to lax and spreading; juvenile rosette leaves linear to oblanceolate; adult leaves with petiole 2 or more times the blade, blade 0.5-4 cm, ovate-rhomboid to subdeltate, acute, rarely mucronate; cauline leaf-disk perfoliate, often notched or divided to the stem on one side; inflorescence usually 5–20-flowered, compact and sessile on the leaf-disk or racemosely elongated up to 5 cm; flowers self-pollinating; sepals 2–3.5 mm, orbicular; petals 2.5–4 mm, white or pinkish; capsule 2.5–3 mm; seeds 3, shiny black, with conspicuous elaiosome; 2n = 24, 36, 48.

berg, N. Amer. Fl. 21: 309. 1932. Montia mexicana (Rydberg) Pax & K. Hoffmann, Nat. Pflanzenfam. ed. 2 16c: 259. 1934. Claytonia tolucana Holub, Preslia 47: 328. 1975. TYPE: Mexico. México: Nevada de Toluca, Rose & Painter 7924 (holotype, US).

- Limnia cuprea Heller, Muhlenbergia 2: 279. 1907, syn. nov. Montia perfoliata forma cuprea (Heller) J. T. Howell, Leafl. W. Bot. 5: 106. 1948. TYPE: U.S.A. California: Monterey County, Pacific Grove, Heller 8501 (holotype, BKL [at NY]; isotypes, DS, NY, WTU).
- Limnia platyphylla Rydberg, N. Amer. Fl. 21: 307. 1932, syn. nov. Montia platyphylla (Rydberg) Pax

This subspecies is distributed widely in the intermontane region east of the Cascade Range, Sierra Nevada, and Peninsular Ranges, from British Columbia to northern Baja California and Arizona, east to the Rocky Mountains. The genetic influence of *Claytonia rubra* is seen in the frequent reddish coloration of the polyploids comprising this taxon, and their characteristic ovate-rhomboid leaf shape is intermediate between the deltoid leaves of *C. rubra* and the linear ones of *C. parviflora*. Furthermore, polyploid *C. parviflora* subspp. *parviflora* and *utahensis* (see below) are frequently sympatric and intergradent with *C. perfoliata* subsp. *intermontana*, in a pattern similar to the intergradation of polyploid *C. perfoliata* subsp. *perfoliata* and *C. parviflora* subsp. *parviflora* in the cismontane region of the Pacific States.

Claytonia rubra (Howell) Tidestrom, Contr. U.S. Natl. Herb. 25: 188. 1925. Basionym: Montia rubra Howell, Erythea 1: 38. 1893. Limnia rubra (Howell) Heller, Muhlenbergia 6: 84. Montia latifolia Suksdorf, Deutsche Bot. Monatsschr. 16: 222. 1898, syn. nov. Claytonia latifolia (Suksdorf) Suksdorf, Werdenda 1: 222. 1923, non Sheldon, 1894. TYPE: U.S.A. Washington: [Klickitat County,] Bingen, Suksdorf 1881 (holotype, WS; isotypes, F, GH, NY, UC, US).

Montia interrupta Suksdorf, Deutsche Bot. Monatsschr.
16: 222. 1898, syn. nov. Claytonia interrupta (Suksdorf) Suksdorf, Werdenda 1: 222. 1923. Limnia interrupta (Suksdorf) Rydberg, N. Amer. Fl. 21: 308. 1932. TYPE: U.S.A. Washington: [Klick-

1910. Claytonia perfoliata Donn ex Willdenow var. rubra (Howell) Poellnitz, Repert. Spec. Nov. Regni Veg. 30: 301. 1932. TYPE: U.S.A. Washington: [Klickitat or Yakima County,]Simcoe (as "Cimcoe") Mountains, June 1880, T. J. Howell s.n. (lectotype, here designated, ORE; isolectotype, US).

Howell cited no type or other specimens in his description of *Montia rubra*. The above lectotypification allows this name to be associated with the common and widespread diploid entity that forms one of the three pillars of the *Claytonia perfoliata* sensu lato polyploid complex. The name *Claytonia parviflora* var. *depressa* A. Gray, which in the literature has often been applied to *C. rubra* subsp. *rubra*, is lectotypified below to apply to a different, itat County,] Bingen, Suksdorf 2009 (holotype, WS; isotypes, F, GH, NY, UC, US).

Claytonia cupulata Suksdorf, Werdenda 1: 11. 1923, syn. nov. TYPE: U.S.A. Washington: [Klickitat County,] Bingen, Suksdorf 10169 (holotype, WS; isotypes, CAS, DS, NY, OSC, UC, US).

Claytonia rubra subsp. depressa differs from subspecies rubra in being wholly polyploid (tetraploid and hexaploid) and in having ovate-elliptic leaf blades rather than deltate, sometimes cordate blades as in subspecies rubra. It is generally found at lower elevations than subspecies rubra, occurring in coastal sandy sites from British Columbia to northern California, as well as interior regions from Washington to northern Nevada and east to Montana. In an earlier paper, it was referred to as the "sagebrush hexaploid" and the "coastal tetraploid" (Miller, 1978: figs. 1, 6). Its foliage may be reddish, as is common in subspecies rubra, or green; the epithet "depressa" is descriptive of its often cushionlike growth form.

wholly polyploid subspecies.

Claytonia rubra (Howell) Tidestrom subsp. depressa (A. Gray) Miller & Chambers, comb. nov. Basionym: Claytonia parviflora Douglas ex Hooker var. depressa A. Gray, Proc. Amer. Acad. Arts 22: 281. 1887. Montia parviflora (Douglas ex Hooker) Howell var. depressa (A. Gray) B. L. Robinson, Syn. Fl. N. Amer. 1: 274. 1897. Montia depressa (A. Gray) Suksdorf, Deutsche Bot. Monatsschr. 16: 221. 1898. Limnia depressa (A. Gray) Rydberg, Bull. Torrey Bot. Club 33: 139. 1906. Claytonia parviflora Douglas ex Hooker subsp. depressa (A. Gray) Piper, Contr. U.S. Natl. Herb. 11: 250. 1906. Montia perfoliata (Donn ex Willdenow) Howell var. depressa (A. Gray) Jepson, Fl. Calif. 1: 471. 1914. Claytonia perfoliata Donn ex Willdenow var. depressa (A. Gray) Poellnitz, Repert. Spec. Nov. Regni Veg. 20: 301. 1932. TYPE: U.S.A. Washington: [San Juan County, San Juan Island, Lyall in 1858 (lectotype, here designated, GH).

Claytonia parviflora Douglas ex Hooker subsp. grandiflora Miller & Chambers, subsp. nov. TYPE: U.S.A. California: Calaveras County, San Antonio Creek S of Sheep Ranch, on the road to Murphy's, *Miller 666* (holotype, OSC; isotypes, CAS, RSA, SD).

A subsp. parviflora floribus allogamis, petalis 4-6 mm quam sepalis duplo triplove longioribus differt.

Plants annual, 5–20 cm tall, sometimes red-pigmented; stems and leaves erect or somewhat spread-

Montia humifusa Howell, Fl. N.W. Amer. 1: 96. 1897, syn. nov. Limnia humifusa (Howell) Rydberg, Fl. Plains N. Amer. 313. 1932. Claytonia humifusa (Howell) Holub, Preslia 47: 328. 1975. TYPE: U.S.A. Oregon: [Umatilla County,] Milton, 18 May 1896, T. J. Howell s.n. (holotype, ORE; isotype, DS). ing; juvenile and adult leaves linear; cauline leafdisk perfoliate, rarely notched or divided; inflorescence longer than the leaves, 5–30-flowered, the flowers racemosely arranged and well exserted above the perfoliate disk; sepals 2–3.5 mm, ovate; petals 4–6 mm, white or pink; stamens releasing pollen 1–2 days before the stigmas are receptive, the breeding system allogamous; capsules 2.5–3 mm; seeds 3, shiny black, with conspicuous elaiosome; 2n = 12.

Of the three morphologically divergent diploid taxa forming the bases for the *Claytonia perfoliata* polyploid complex, *C. parviflora* subsp. grandiflora

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is the only one having an outcrossing, self-incompatible breeding system. A similar floral syndrome and breeding system occur in the diploid annual species *C. gypsophiloides*, a basal and putatively primitive element in the *C. exigua* polyploid complex. *Claytonia parviflora* subsp. *grandiflora* occupies a natural range in the mixed oak-pine woodlands on the western slopes of the Sierra Nevada at 150-1,200 m elevation. It sometimes is sympatric 328. 1975. Claytonia perfoliata Donn ex Willdenow subsp. viridis (Davidson) Fellows, Madroño 23: 297. 1975. TYPE: U.S.A. California: Los Angeles County, San Gabriel Mountains, Big Rock Creek, Hasse & Davidson 1507 (holotype, LAM [at RSA]; isotype, GH).

Claytonia tenuifolia Torrey & A. Gray, Fl. N. Amer. 1: 201. 1838, syn. nov. Claytonia spathulata Douglas ex Hooker var. tenuifolia (Torrey & A. Gray) A. Gray, Proc. Amer. Acad. Arts 22: 282. 1887. Montia tenuifolia (Torrey & A. Gray) Howell, Erythea 1: 38. 1893. Limnia tenuifolia (Torrey & A. Gray) Rydberg, N. Amer. Fl. 21: 313. 1932. Montia spathulata (Douglas ex Hooker) Howell var. tenuifolia (Torrey & A. Gray) Munz, Man. S. Calif. Bot. 598. 1935. TYPE: U.S.A. California: Douglas s.n. (lectotype, here designated, GH; isolectotype, NY).

with polyploid, autogamous races of subspecies parviflora.

Claytonia parviflora Douglas ex Hooker subsp. utahensis (Rydberg) Miller & Chambers, comb. nov. Basionym: Limnia utahensis Rydberg, Bull. Torrey Bot. Club 39: 314. 1912. Claytonia utahensis (Rydberg) Tidestrom, Contr. U.S. Natl. Herb. 25: 188. 1925. Claytonia perfoliata Donn ex Willdenow var. utahensis (Rydberg) Poellnitz, Repert. Spec. Nov. Regni Veg. 30: 302. 1932. Montia utahensis (Rydberg) Pax & K. Hoffmann, Nat. Pflanzenfam. ed. 2 16c: 259. 1934. Montia perfoliata (Donn ex Willdenow) Howell var. utahensis (Rydberg) Munz, Aliso 4: 90. 1958. TYPE: U.S.A. Utah: [Washington County,] St. George, Palmer in 1877 (holotype, NY).

Fellows (1975) demonstrated that the above taxon is not related to the Claytonia exigua speciescomplex, as had earlier been assumed by most botanical authors. Instead, it is a member of the C. perfoliata complex sensu lato, based on its seed morphology (smooth, shiny testa and enlarged elaiosome), nonglaucous herbage, and chromosome base number (x = 6, 2n = 24, 36). Although placed in C. perfoliata by Fellows, it better belongs with C. parviflora because its rosette leaves range from linear to narrowly oblanceolate. The cauline leaf pair strikingly mimics that of C. exigua, often being linear, divergent, and unfused (e.g., the type specimens of C. tenuifolia, cited above; Miller, 1978: figs. 14, 16) or partly fused on one side to form a crescent-shaped or two-pronged disk. This latter type of disk is present on the specimens comprising the holotype and isotype sheets of M. spathulata var. viridis, and these plants' basal leaves have a broader blade than is usual for the subspecies. The San Gabriel Mountains, along with other units of the Transverse Ranges of southern California, contain diverse morphological forms of the C. perfoliataparviflora-rubra complex; these include diploids as well as several variable polyploids. Leaf-shape variation in subspecies viridis may be due to introgression from some broader-leaved taxa like subspecies mexicana or subspecies rubra. Other populations have been found in this region that may represent diploid introgressants of C. perfoliata with C. rubra (Miller, pers. obs.). It is not yet clear whether any additional entities within this hybrid complex are worthy of taxonomic recognition; at present, we prefer the broadly defined, and hence more variable, taxa outlined in this report. Claytonia tenuifolia is a notable addition to the synonymy of C. parviflora subsp. viridis, above. Since the time of Asa Gray, almost all authors deal-

Claytonia parviflora subsp. utahensis comprises populations of generally diminutive plants whose spathulate to narrowly lanceolate adult leaf blades are 4 mm or more wide, and which occupy the Peninsular and Desert ranges of southern California, extending north on the east flank of the Sierra Nevada and east to southern Nevada, Utah, and northern Arizona. The plants are autogamous and principally tetraploid. Intergradent populations have been noted between this subspecies and both *C. perfoliata* subsp. *intermontana* and *C. parviflora* subsp. *viridis* (see below).

Claytonia parviflora Douglas ex Hooker subsp.

viridis (Davidson) Miller & Chambers, comb. nov. Basionym: Montia spathulata (Douglas ex Hooker) Howell var. viridis Davidson, Bull. S. Calif. Acad. Sci. 5: 61. 1907. Montia exigua (Torrey & A. Gray) Jepson var. viridis (Davidson) Jepson, Fl. Calif. 1: 473. 1914. Claytonia exigua Torr. & A. Gray var. viridis (Davidson) Poellnitz, Repert. Spec. Nov. Regni Veg. 30: 313. 1932. Limnia viridis (Davidson) Rydberg, N. Amer. Fl. 21: 313. 1932. Claytonia spathulata Douglas ex Hooker var. viridis (Davidson) Munz, Fl. S. Calif. 713. 1974. Claytonia viridis (Davidson) Holub, Preslia 47: ing with the flora of California have associated this name with plants referable to *Claytonia exigua* (*C. spathulata* of previous treatments). However, the type specimens at GH and NY, collected by David Douglas at some unknown site in California, surprisingly prove not to belong to the latter species. Although they are similar to *C. exigua* in habit, their seed morphology is unequivocally that of *C. parviflora*. For any combinations made at the varietal level, therefore, the epithet *tenuifolia* has priority.

on by Fellows (1975) in his discussion of C. parviflora subsp. viridis. That C. exigua includes plants with a completely perfoliate disk, as well as those with a deeply two-lobed disk or with separate cauline leaves, was known to Thomas Howell (1893), who included in his description (under Montia spathulata, p. 38) the phrase "involucral bracts . . . wholly united and the disk shorter on one side " By later authors, however, subspecies glauca has either been described as a separate species or submerged in C. perfoliata. It may be useful to clarify the synonymy, cited here and elsewhere, from the publications of Wilhelm Suksdorf. For the new taxa he described in 1898 in the Deutschen Botanischen Monatsschrift, Suksdorf gave first a collection number and a name in the genus Claytonia, followed by an equal sign and a name in the genus Montia. Rydberg and other authors have cited these two names as co-equal, as though both were validly published. However, Suksdorf's 1923 paper in Werdenda makes clear that only the names in Montia were intended to be published in 1898; in fact, the 1923 paper contains many transfers of these taxa from Montia back to Claytonia. The names in Claytonia given in Suksdorf's 1898 paper were merely references to the herbarium labels he used in distributing his collections, prior to the revision of Montia by Howell in 1893.

Claytonia exigua Torrey & A. Gray subsp. glauca (Torrey & A. Gray) Miller & Chambers, comb. nov. Basionym: Claytonia parviflora Douglas ex Hooker [var.] β glauca Torrey & A. Gray, Fl. N. Amer. 1: 200. 1838. Limnia glauca (Torrey & A. Gray) Rydberg, N. Amer. Fl. 21: 311. 1932. Montia perfoliata (Donn ex Willdenow) Howell subsp. glauca (Torrey & A. Gray) Ferris, Ill. Fl. Pacific States 2: 127. 1944. Montia perfoliata (Donn ex Willdenow) Howell forma glauca (Torrey & A. Gray) J. T. Howell, Leafl. W. Bot. 5: 106. 1948. TYPE: U.S.A. [Oregon:] "Oregon R.," Nuttall s.n. (lectotype, here designated, GH; probable iso-

- lectotype, NY [labeled "Rocky plains of Wahlamet"]).
- Montia spathulata (Douglas ex Hooker) Howell var. disciformis Suksdorf, Deutsche Bot. Monatsschr. 16: 222. 1898, syn. nov. Claytonia spathulata Douglas ex Hooker var. disciformis (Suksdorf) Suksdorf, Werdenda 1: 10. 1923. TYPE: U.S.A. Washington: Klickitat County, Major Creek between Bingen and Lyle, Suksdorf 2095 (holotype, WS; isotypes, F, GH, NY, UC, US).
- Montia pallida M. Peck, Proc. Biol. Soc. Wash. 47: 185-186. 1934, syn. nov. TYPE: U.S.A. Oregon: [Marion or Polk County,] near Salem, Peck 1699 (holotype, WILLU [at OSC]).

The name Claytonia exigua Torrey & A. Gray, of 1838, must replace the earlier C. spathulata Douglas ex Hooker, 1832, because the latter is a homonym of C. spatulata Eaton, 1824. The epithet glauca was attributed by Torrey and Gray to "Nutt.! mss." but Nuttall's tags on the type sheets show he intended the name for a variety of C. gypsophiloides rather than C. parviflora as was published in Flora of North America. Hence the basionym should not be attributed to "Nuttall ex Torrey & A. Gray." The subspecies is entirely diploid (2n =16) and forms the perfoliate leaf-disk equivalent, within C. exigua, of C. perfoliata. The differences in habit, chromosome number, and seed morphology between these two species-complexes were touched Acknowledgments. We thank Charles Fellows for contributions to the research, John McNeill for bibliographic advice and assistance, and the curators of the cited herbaria for making available type collections and photographs. Our research was supported by National Science Foundation grant BSR 8600117.

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